ACIDIC PRECIPITATION IN ONTARIO STUDY

WATER QUALITY - CRUSTACEAN PLANKTON RELATIONSHIPS IN NORTHEASTERN ONTARIO LAKES

A.P.I.O.S. REPORT No. 002/83

Ontario
Ministry of the Environment

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by

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SUMMARY

During the summer of 1981, crustacean plankton was sampled in 249 northeastern Ontario lakes, including a large proportion of acidic lakes. Species cluster analysis showed that overall, the lakes were typified by a major species group containing B. longirostris, D. minutus, H. gibberum and M. edax which was common to most lakes. Two species subgroups most associated with more productive waters (D. retrocurva, D. oregonensis, T. p. mexicanus and Diaphanosoma sp.) and less productive waters (D. longiremis, C. scutifer, D. g. mendotae, C. b. thomasi, E. longispina and E. lacustris) in the study area were identified. Acidic lakes were characterized by reduced numbers of species related to declines in the importance of cyclopoids, Daphnidae, L. kindtii and E. lacustris and high relative abundance of D. minutus. The observed general community alterations (ie. apparent shift from larger (Daphnidae) to smaller (D. minutus) grazers and scarcity of predatory plankton) may have important implications to energy cycling in acidic lakes. Stepwise multiple linear regression analysis of physico-chemical lake characteristics against percent composition of individual species failed to explain much of the variation in species proportions, accounting for on average, only 11% of the variation among near-neutral lakes and 25% in highly or slightly acidic lakes . Of the limnological characteristics considered, variables related

to lake thermal structure were most frequently the primary correlates with species proportions in near-neutral lakes while in acidic lakes the best statistical predictors of species percent composition were most often variables directly related to lake acidity.

INTRODUCTION

Although on a broad geographical scale glacial history may influence lentic zooplankton communities, (Carter et al. 1980; Roff et al. 1981) regional studies in Ontario (Carter 1971; Patalas 1971; Sprules 1975 and Sprules 1977) have demonstrated general relationships between lake chemistry and/or morphometry and crustacean species assemblages.

Hydrogen ion has long been recognized as a factor influencing the structure and diversity of crustacean plankton communities (Lowndes 1952). Restricted crustacean faunas have been found in naturally acidic freshwater bodies (Fryer 1980) as well as in manmade impoundments acidified by acid inputs from coal mining activity (DeCosta 1975; Janicki and DeCosta 1979). Reductions in zooplankton community diversity in lakes acidified due to acidic precipitation have been identified in Norway (Leivestad et al. 1976), Sweden (Almer et al. 1974), the USA (Confer, Kaaret and Likens 1983) and Ontario (Sprules 1975; Roff and Kwiatkowski 1977).

For decades, aquatic environments in the Sudbury, Ontario area have been subjected to atmospheric inputs of contaminants associated with large-scale, local smelting activity. Investigations in the greater Sudbury area (Beamish and Harvey, 1972; Conroy, Hawley and Keller 1978) have documented a large zone of acidified lakes extending northeast-southwest of Sudbury. Many Sudbury area lakes also exhibit elevations in trace metal concentrations related to smelting activity (Cu, Ni) or to increased metal dissolution and mobilization from watersheds under acidic conditions (Al, Mn).

This report examines associations between lake water quality and crustacean plankton communities in 249 lakes, including a large proportion of acidic lakes, within a 250 km radius of Sudbury (Figure 1).

THE STUDY LAKES

Although predominantly on the Precambrian Shield, the lakes studied vary in chemistry, morphometry and surficial geological setting, spanning a cross-section of lake types occurring in northeastern Ontario. Pitblado, Keller and Conroy (1980) have divided northeastern Ontario lakes into 7 groups based on principal components and hierarchical cluster analyses of 23 limnological variables. The lake groups derived are briefly described below.

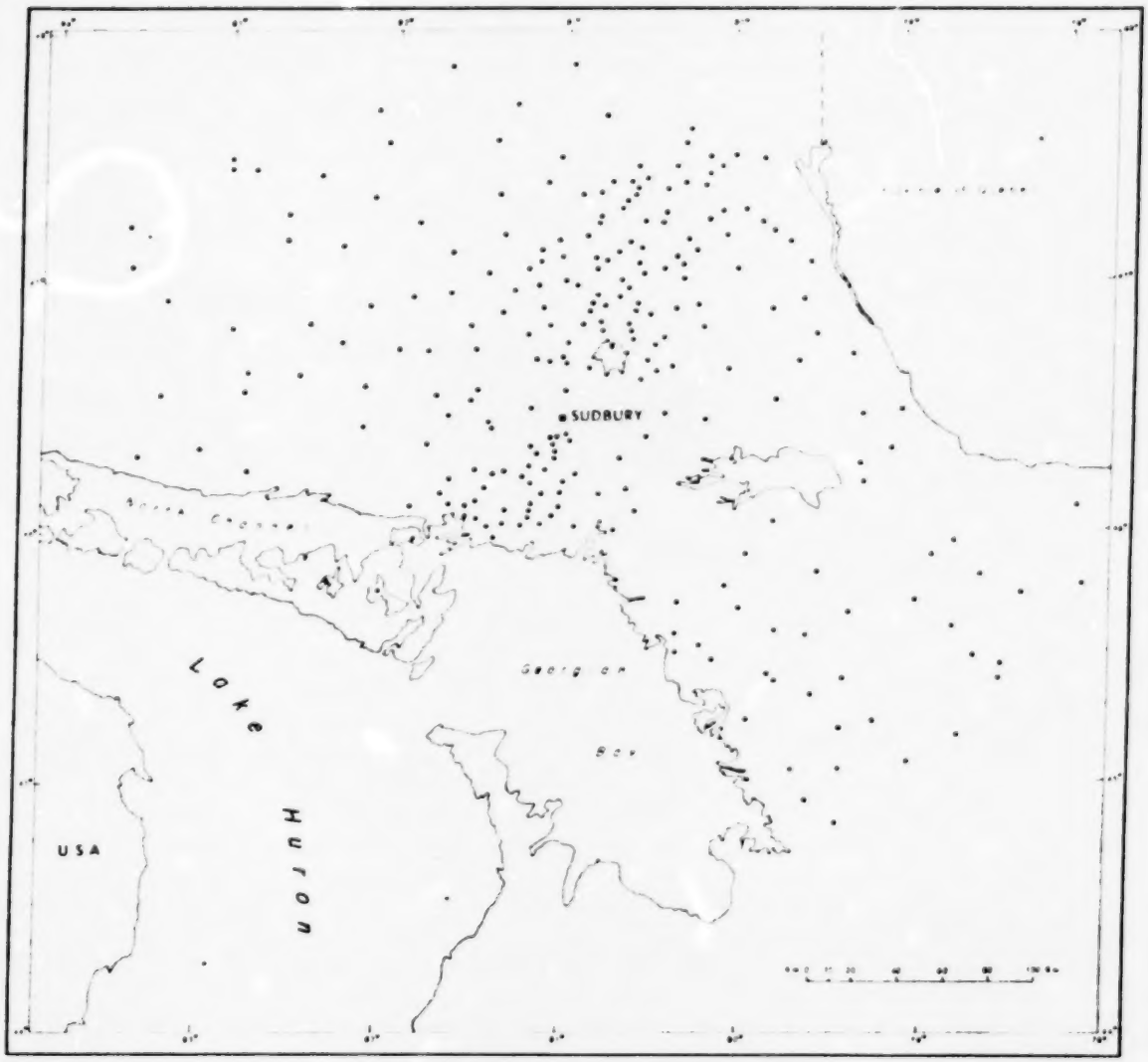

Figure 1. Locations of the study lakes.

Group 1

The lakes in this group are near-neutral and are typified by high concentrations of nitrogen and phosphorus and low Secchi disc transparency in comparison to the other lake groups. Concentrations of trace metals related to smelting activity (Cu, Ni) are elevated in the lakes closest to Sudbury.

Groups 2 and 3

Lake groups 2 and 3 include the characteristic highly dilute, near-neutral lakes of the Precambrian Shield. Differentiation between the groups is based primarily on nutrient status with Group 3 lakes exhibiting generally lower nutrient concentrations and higher transparency than Group 2 lakes. Concentrations of trace metals are low in both lake groups.

Groups 4, 5 and 6

These groups encompass a related set of clear, nutrient-poor lakes which show impacts (ranging from severe to minimal) associated with emissions from the Sudbury smelting industry. Group 4 lakes show slightly elevated concentrations of sulphate and trace metals indicating a slight impact by Sudbury emissions; however, these lakes are

inherently more buffered and more productive than lakes in groups 5 and 6 reflecting high assimilation capacity for acidic inputs. Group 6 lakes are very clear, poorly buffered and slightly acidic. Trace metal concentrations related to smelter emissions (Cu, Ni) are often slightly elevated. Group 5 contains the lakes which have been most strongly influenced by Sudbury emissions. Group 5 lakes are typically extremely clear and highly acidic with elevated concentrations of trace metals related to watershed inputs (Al, Mn). Concentrations of Cu and Ni are very high in the lakes closest to Sudbury due to smelter emissions.

Group 7

These lakes show atypically high (for the study area) ionic strength related to occurrence of calcareous bedrock/overburden or inputs of urban runoff and exhibit wide variation in trophic state and trace metal concentrations.

Table 1 summarizes the average physico-chemical charactertistics of the study lakes on the basis of the above groups. Although based on water chemistry, the grouping system also provides some discrimination of physical lake characteristics (Table 1) since in general, lake trophic status and thermal structure are related to morphometry.

TABLE 1

Average values of physico-chemical variables for lake groups defined by water chemistry.

	Lake Group (n)						
	1(23)	2(49)	3(59)	4(22)	5(32)	6(57)	7(8)
Area (ha)[a]	3974	656	786	496	273	1391	2281
Depth (m)[b]	11	14	28	18	21	21	13
pH	6.6	6.5	6.6	6.9	4.7	5.9	7.9
Conductivity (µS/cm)	55	41	42	66	50	45	210
Alkalinity (mg/L as $CaCO_3$)[c]	9.03	5.37	5.71	13.71	-1.31	2.03	73.88
Calcium (mg/L)	5.0	3.7	3.8	6.8	3.4	4.0	20.6
Magnesium (mg/L)	1.64	1.02	1.10	1.87	0.98	1.14	6.77
Sodium (mg/L)	1.7	1.3	1.1	1.2	1.9	1.1	5.2
Potassium (mg/L)	0.67	0.50	0.43	0.54	0.43	0.43	0.77
Sulphate (mg/L)	11.1	8.9	9.4	12.0	13.5	12.8	15.9
Silica (mg/L)	0.90	1.31	1.06	1.32	0.90	0.92	0.97
Chloride (mg/L)	1.88	1.25	0.91	0.90	3.00	1.02	9.52
Total Nitrogen (µg/L)	508	356	242	303	215	200	273
Total Phosphorus (µg/L)	19	10	6	10	5	5	9
Total Zinc (µg/L)	5	3	3	3	18	8	2
Total Copper (µg/L)	4	1	1	3	27	3	4
Total Nickel (µg/L)	15	3	2	9	61	15	23
Total Iron (µg/L)	153	134	45	87	95	62	45
Total Aluminum (µg/L)	60	53	31	62	310	60	44
Total Manganese (µg/L)	52	37	18	23	185	60	9
Color (Hazen)	34.2	31.4	14.3	21.2	10.6	7.7	6.1
Secchi disc (m)	3.1	3.7	6.8	4.6	10.6	7.1	7.4
Epilimnion thickness (m)	3.3	3.8	5.1	4.3	5.0	4.6	4.4
Hypolimnion thickness (m)	2.6	4.9	15.9	7.9	8.0	9.0	3.2
Deep-water temperature (°C)[d]	12.9	11.0	7.7	9.2	11.8	9.8	11.3

[a] excluding 5 very large lakes with A_o>10,000 ha
[b] depth at sampling station
[c] total inflection point alkalinity
[d] temperature at the top of the hypolimnion or 1m above the lake bottom in shallow lakes

METHODS

DATA COLLECTION

Each lake was sampled once at a central location during the period June 15th to August 14th, 1981. Sampling visits were scheduled such that lakes within a given geographical portion of the study area were sampled at different times throughout the study. Crustacean plankton samples were collected as single vertical net (12.5 cm diameter; 76 μ mesh) hauls from one m above bottom to surface in each lake. Two hundred and six lakes were sampled with a flow-meter-equipped net, allowing calculation of filtration efficiency. The remaining lakes (n = 43) were sampled with a non-metered net. Samples were immediately preserved with 5% buffered formalin. Identification and enumeration procedures followed those outlined in Yan and Strus (1980).

Water samples were collected as water column composites by the tygon tube method (Ministry of the Environment (MOE) 1979). Nutrient samples were collected through the euphotic zone estimated as twice the Secchi disc transparency plus one m. Samples for other chemical analyses were taken to the lower limit of the metalimnion, defined as the depth below the region of greatest temperature change at which the observed temperature decrease was less than or equal to 0.5°C/m. Points of inflection of lake temperature profiles and respective temperatures were measured with a YSI Model 43TD telethermometer.

Samples were placed in sample-rinsed containers (250 ml polystyrene for nutrients; 500 ml acid washed polyethylene for trace metals - HNO_3 preserved; and 500 ml polystyrene for pH and major ion analyses) for transportation to the laboratory. Conductivity, pH and alkalinity (total inflection point) determinations were completed at the Sudbury MOE laboratory on the day following collection (after overnight refrigeration). Other analyses were carried out at the MOE Laboratories in Toronto following procedures outlined in MOE (1981).

STATISTICAL ANALYSIS

The data array examined for this paper consisted of 35 physico-chemical variables and 39 zooplankton species for each of the 249 study lakes. Statistical analyses of the data were done at Laurentian University using the SPSS package of computer routines (Nie et al. 1975; Hull and Nie 1981) and a number of FORTRAN programs written by JRP. The major statistical approaches that were employed are outlined below.

The relative abundance of species in a lake formed the major part of the zooplankton portion of the data array. The number of individuals of a particular species found in a lake was expressed as a percentage of the total number of individuals (excluding nauplii) of all zooplankton species,

with calanoid and cyclopoid copepodids (only identified to suborder) apportioned according to the relative abundance of their adult forms in the respective groups of Copepoda. Zooplankton densities were computed, expressed as the number of individuals per litre for each species, and summed to obtain total densities for individual lakes. Density computations were undertaken only for the 206 lakes sampled by metered hauls.

Examination of the zooplankton data set for any biases introduced by the sampling format (i.e. single samples over a 2 month period) indicated the data did accurately reflect changes in community composition across the range of lake types. Comparison of the present data with data for 187 of the lakes which were sampled more frequently (2 - 7 times) during 1974-76 (Keller 1981) showed similar lake group averages for species occurrence and percent composition. Linear regression analyses of species richness, density and percent composition against sampling date did not show any significant correlations, and inspection of the scattergrams did not reveal any non-linear relationships between attributes of the zooplankton communities and time.

In an earlier paper (Pitblado et al. 1980), 187 lakes of the Sudbury area were classified, as indicated previously, using 23 physico-chemical variables, reduced to four components using principal components analysis. Ninety percent of the variance between the lakes could be explained by these components, labeled as: Nutrient Status, Buffering Status, Atmospheric Deposition Status and Sodium-Chloride Status.

The classification procedure used in that study involved the computation of factor scores for each of the lakes for each of the four components and then using those scores in a series of cluster analysis, multiple discriminant analysis, and multivariate analysis of variance.

For the present study, using the same 23 variables and the earlier factor score coefficient matrix, factor scores were computed for the 249 lakes. Then the assignment procedure of the SPSS multiple discriminant analysis routine was employed to classify the current study lakes. The only departure from this approach was our overriding assignment of all lakes with pH <5.0 to Group 5, and lakes with pH between 5.0 and 5.5 to Group 6, a step undertaken to hold the influence of pH (considered a major variable potentially influencing biotic systems) relatively constant. Although this resulted in reassignment of a small number of lakes this departure had very little overall effect on the results of the discriminant analysis assignments. Principal components analysis of the 1981 data using those same 23 variables produced results consistent with those reported earlier (Pitblado et al. 1980).

In order to guide our analyses of the relationships of species relative abundance with physico-chemical variables, forward stepwise multiple regression analyses were undertaken. The independent variables were initially chosen

from those variables that had high relative loadings on the first three principal components described in more detail in Pitblado et al. (1980). This list was reduced in number by dropping or combining variables in order to avoid problems of multicollinearity. Thus, the Nutrient Status component was represented by total nitrogen (the sum of total Kjeldahl nitrogen, nitrite, and nitrate), total phosphorus, and Secchi depth; Buffering Status was represented by pH and alkalinity; and the Atmospheric Deposition component was represented by copper. Lake morphometry variables important in the earlier study and included in this step of the analysis were lake surface area and bottom depth.

To this list of 8 independent variables were added aluminum, hypolimnion thickness, deep-water temperature, and epilimnion thickness. It should be noted that the temperature-related parameters used provide only a very general indication of variations in thermal characteristics among the lakes. The latter variables were not available for the earlier study but were included herein because they potentially play important roles in influencing the distribution and abundance of zooplankton. Other variables might also have been added using this criteria, but the overall list of independent variables was selected by keeping high intercorrelations to a minimum and thus reducing the chances of spurious multiple correlations being derived due to multicollinearity. The final list of

independent variables was also arrived at after considering the problem of bell-shaped or horseshoe-shaped distributions often common to this type of data (Austin and Noy-Meir 1971; Roff et al. 1981). This was done by inspecting the scattergrams of each of the independent variables with each of the zooplankton species, and by undertaking the multiple regression analyses using two sub-sets of data. The first sub-set included only lakes in Group 5 and Group 6; the second included the lakes in groups 1, 2, 3, and 4. Examination of the scattergrams indicated that species responses were essentially linear within these lake subsets.

Zooplankton community structure was determined using species presence/absence data in a hierarchical cluster analysis. This approach, using Euclidean distance squared as a measure of dissimilarity (Sokal and Sneath 1963; Sneath and Sokal 1973; Clifford and Stephenson 1975), and the Ward's error clustering algorithm (Ward 1963; Frenkel and Harrison 1974; Mather 1976), clearly differentiated the recurring patterns of the most common zooplankton species. The less common species were assigned to the major zooplankton communities using a computer program written to highlight the coexistence of those species with the major species clusters.

RESULTS AND DISCUSSION

GENERAL SPECIES DISTRIBUTIONS

A total of 39 species (24 genera) of Crustacea, including 24 representatives of Cladocera and 15 species of Copepoda were collected from the plankton of the study lakes (Table 2). Among the Copepoda, 8 calanoid and 7 cyclopoid forms were found.

Diaptomus minutus and Bosmina longirostris were the most frequently occurring species found in over 80% of the lakes, with Holopedium gibberum, Cyclops bicuspidatus thomasi, Mesocyclops edax, Diaphanosoma sp., and Daphnia galeata mendotae slightly less common occurring in 56 to 74% of the lakes. Species present in 25 to 50% of the lakes included Daphnia retrocurva, Cyclops scutifer, Diaptomus oregonensis, Daphnia longiremis, Tropocyclops prasinus mexicanus, Epischura lacustris, and Eubosmina longispina while Eubosmina tubicen, Daphnia catawba, Daphnia ambigua, Daphnia pulex, Chydorus sphaericus, Daphnia dubia, Leptodora kindtii, Ceriodaphnia lacustris, Cyclops vernalis, Polyphemus pediculus and Senecella calanoides were present in 5 to 21%. The remaining species collected (Table 2) were comparatively rare, occurring in <5% of the lakes.

TABLE II

Relative occurrence of crustacean plankton
Species in 249 Northeastern Ontario Lakes.

	% of Lakes
Diaptomus minutus Lilljeborg	85
Bosmina longirostris (O.F. Müller)	84
Holopedium gibberum Zaddach	74
Cyclops bicuspidatus thomasi (S. A. Forbes)	64
Mesocyclops edax (S. A. Forbes)	64
Diaphanosoma sp.	61
Daphnia galeata mendotae Birge	56
Daphnia retrocurva S. A. Forbes	43
Cyclops scutifer Sars	41
Diaptomus oregonensis Lilljeborg	40
Daphnia longiremis Sars	38
Tropocyclops prasinus mexicanus Kiefer	35
Epischura lacustris S. A. Forbes	33
Eubosmina longispina (Leydig)	33
Eubosmina tubicen (Brehm)	21
Daphnia catawba Coker	19
Daphnia ambigua Scourfield	17
Daphnia pulex Leydig emend. Richard	14
Chydorus sphaericus (O. F. Müller)	13
Daphnia dubia Herrick	12
Leptodora kindtii (Focke)	10
Ceriodaphnia lacustris Birge	8
Cyclops vernalis (Fischer)	8
Polyphemus pediculus (Linné)	8
Senecella calanoides Juday	6
Sida crystallina (O.F. Müller)	4
Diaptomus sicilis S. A. Forbes	3
Limnocalanus macrurus Sars	2
Orthocyclops modestus (Herrick)	2
Ceriodaphnia pulchella Sars	1
Acroperus harpae Baird	<1
Alona quadrangularis (O. F. Müller)	<1
Diaptomus ashlandi Marsh	<1
Diaptomus sanguineus S. A. Forbes	<1
Eubosmina coregoni (Baird)	<1
Eucyclops agilis (Koch)	<1
Latona setifera (O. F. Müller)	<1
Ophryoxus gracilis Sars	<1
Simocephalus serrulatus (Koch)	<1

Comparison of data from the present study with data from other synoptic surveys in eastern Canada (Rigler and Langford 1967; Patalas 1971; Brandlova, Brandl and Fernando 1972; MOE 1973, 1975; Sprules 1976; Pinel-Alloul, Legendre and Magnin 1979; Carter et al. 1980; Jermolajev and Fraser 1982; and Joubert and Tousignant MS) showed general similarity in species occurrence, with the species most common in our study generally occurring frequently in other extensive regional surveys. Of the 25 species present in >5% of our lakes, 19, 20, and 24 species respectively occurred in the ELA lakes of northwestern Ontario (Patalas 1971), lakes in the arctic watershed of Ontario (MOE 1973, 1975) and Quebec lakes south of the 52nd parallel (Joubert and Tousignant MS). Ten and 13 of these species are also present in the plankton of the Great Lakes (Superior and Huron respectively) which adjoin the study area (Watson 1974).

Examination of maps depicting species presence/absence in the study lakes (available from the authors on request) showed no apparent geographical patterns in species distributions within our study area.

SPECIES RICHNESS AND DENSITY

Within individual lakes, the total number of crustacean species collected varied from 0 (one lake) to 17 with an overall average of 9.1 species per lake (Figure 2), identical to the average number of species per lake of 9.1 for single collections from 45 ELA lakes (Patalas 1971).

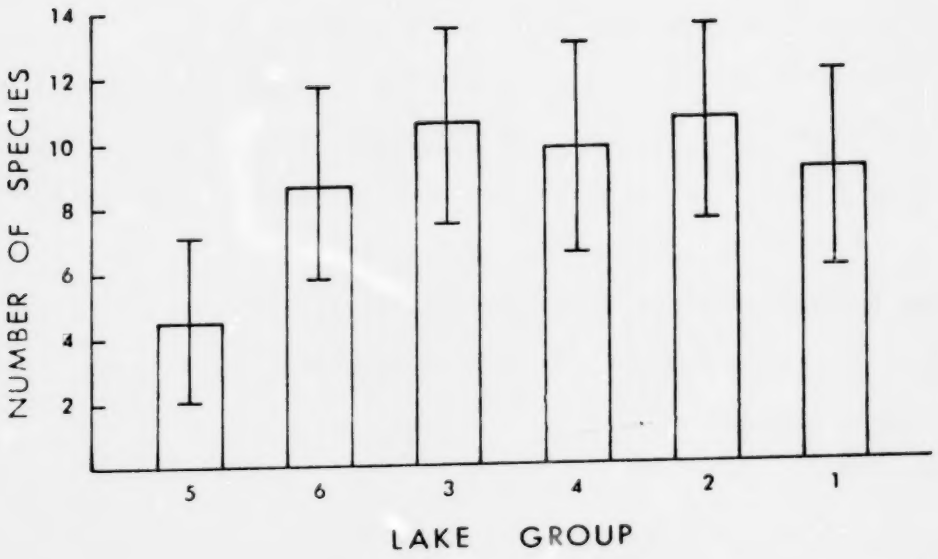

Figure 2. Average and standard deviation of the number of crustacean plankton species in lake groups defined by water chemistry. Lake groups are arranged in order of generally increasing trophic status and pH. Group 7 lakes have been excluded since they showed widely varying trophic status.

Species richness was much lower in acidic Group 5 lakes (average 4.5 species per lake) than in lakes within other groups (group averages of 8.5 to 10.5 species per lake) similar to the results of other investigations within the same portion of Ontario. Elimination of very scarce species (<0.1% of density in individual lakes) from our data set only slightly altered average species richness (4.3 species per lake in Group 5; 8.4 to 10.4 species per lake in other groups). Sprules (1975), based on single collections from 47 LaCloche Mountain lakes, reported 1 to 7 species in lakes with pH<5.0 and 9 to 16 species in lakes with pH >5.0. Yan and Strus (1980) reported averages of 2.9 to 3.9 species per collection from four highly acidic, metal-contaminated lakes near Sudbury while in the same study average species richness ranged from 7.0 to 14.6 species per collection in 6 near-neutral central Ontario lakes and one near-neutral lake near Sudbury.

Average crustacean density varied widely (Figure 3), but was greatest in the most nutrient rich Group 1 lakes (35 animals/L) and least in acidic Group 5 lakes (15 animals/L). Roff and Kwiatkowski (1977) have previously reported low crustacean densities in acidic lakes. Our average observed densities are similar to the range reported by Yan and Strus (1980) for 6 near-neutral, oligotrophic lakes (18.2 to 45.5 animals/L). It must be noted that our data are based only on point-in-time, summer samples while the data of Yan and

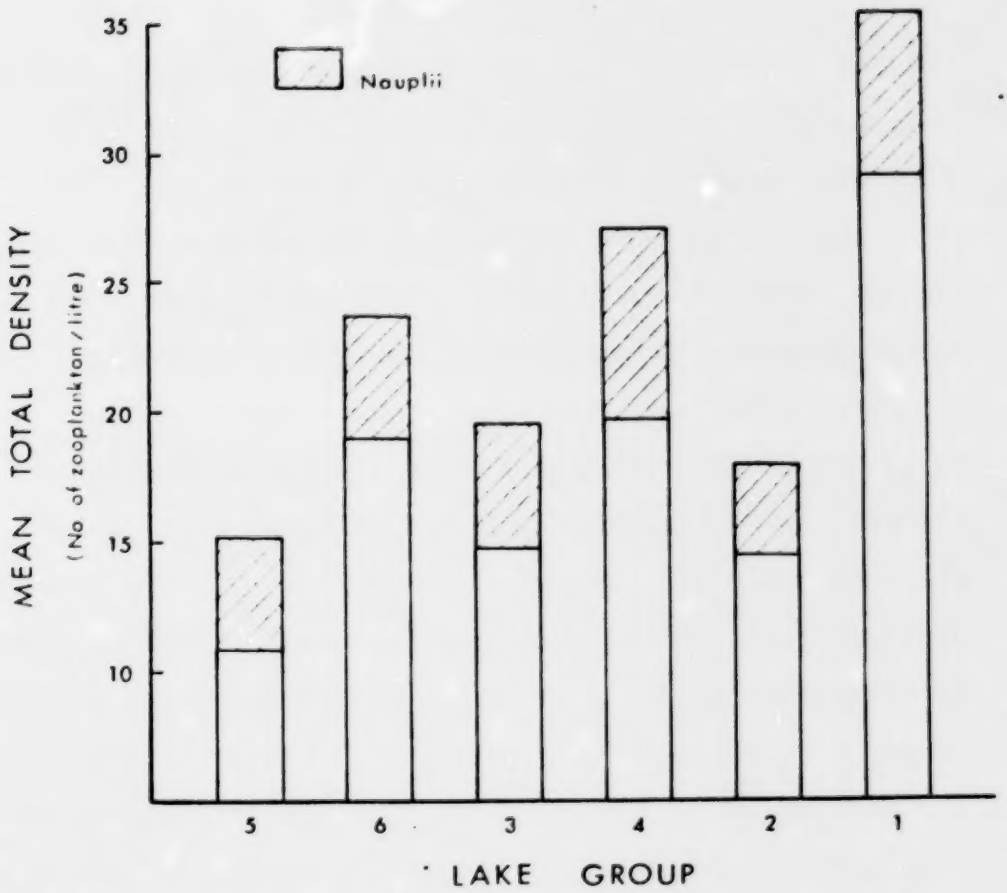

Figure 3. Average crustacean density in lake groups defined by water chemistry.

Strus (1980) represent ice-free period averages for very frequently collected samples. However, mid-summer collections seem to provide a reasonable estimate of ice-free period average densities (Yan unpublished data).

SPECIES - LAKE TYPE ASSOCIATIONS

Figures 4 to 7 present the average frequency of occurrence and relative abundance when present of relatively common (>5% of the study lakes) species utilizing the lake groups of Pitblado et al. (1980) as integrators of similar physico-chemical conditions. The groups are arranged in order of generally increasing trophic status and pH. Group 7 lakes have been excluded since they exhibited widely varying trophic status. Both relative abundance when present and frequency of occurrence were chosen for presentation to allow evaluation of the relative constribution of each of these factors to general species importance within lake groups. The overall average percent composition of species in lake groups can be determined from the data given in Figures 4 to 7 by multiplying the percent composition indicated by the frequency of occurrence expressed as a fraction. In some cases comparatively rare species were numerically prominent when present; however, in most cases data on species occurrence and relative abundance are complementary providing a basis for characterization of the apparent environmental preferences/limitation of species within the study area.

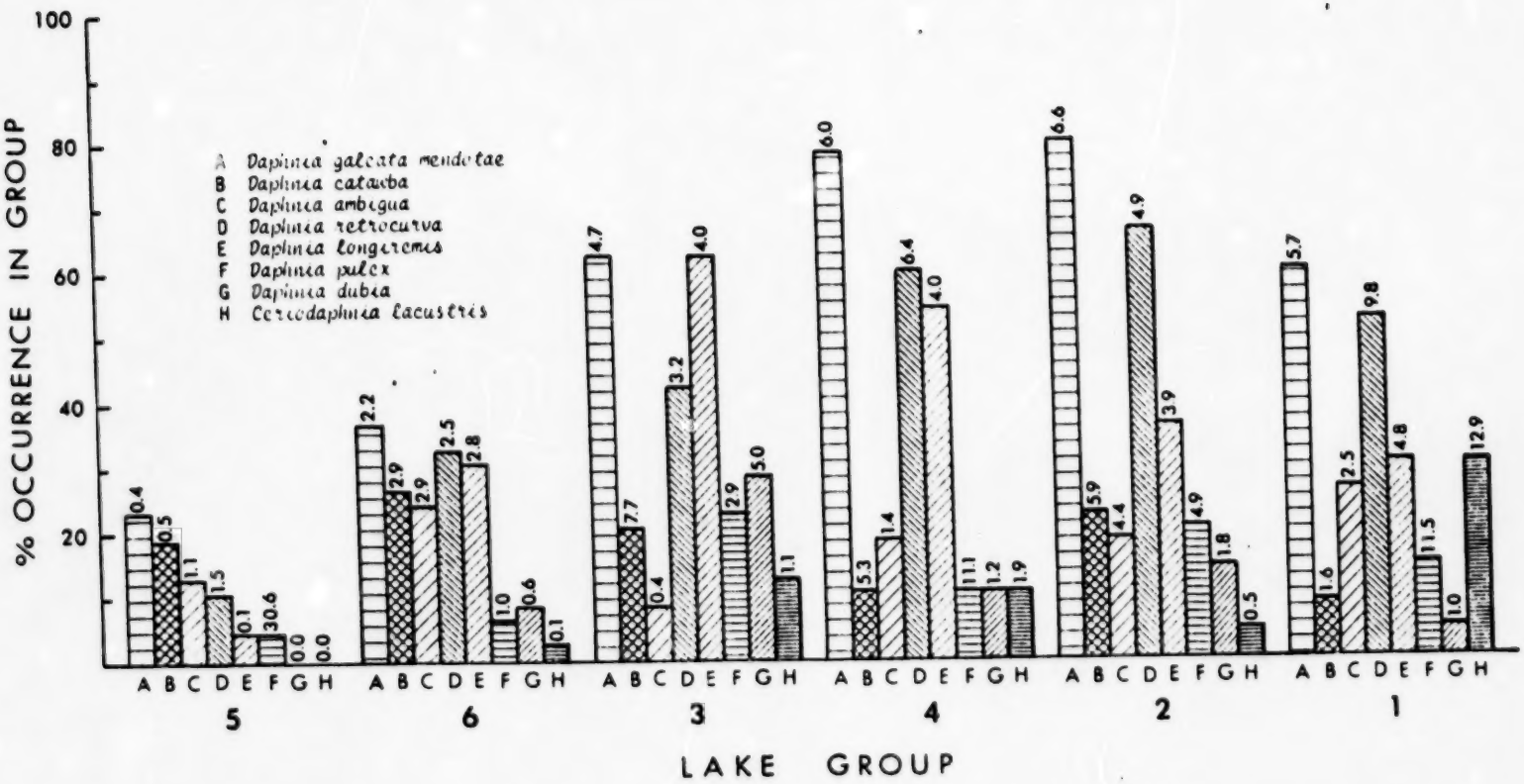

Figure 4. Frequency of occurrence in lake groups (vertical bars) and average % contribution when present to crustacean density excluding nauplii (numbers above bars) of common Daphnidae (present in >5% of the study lakes).

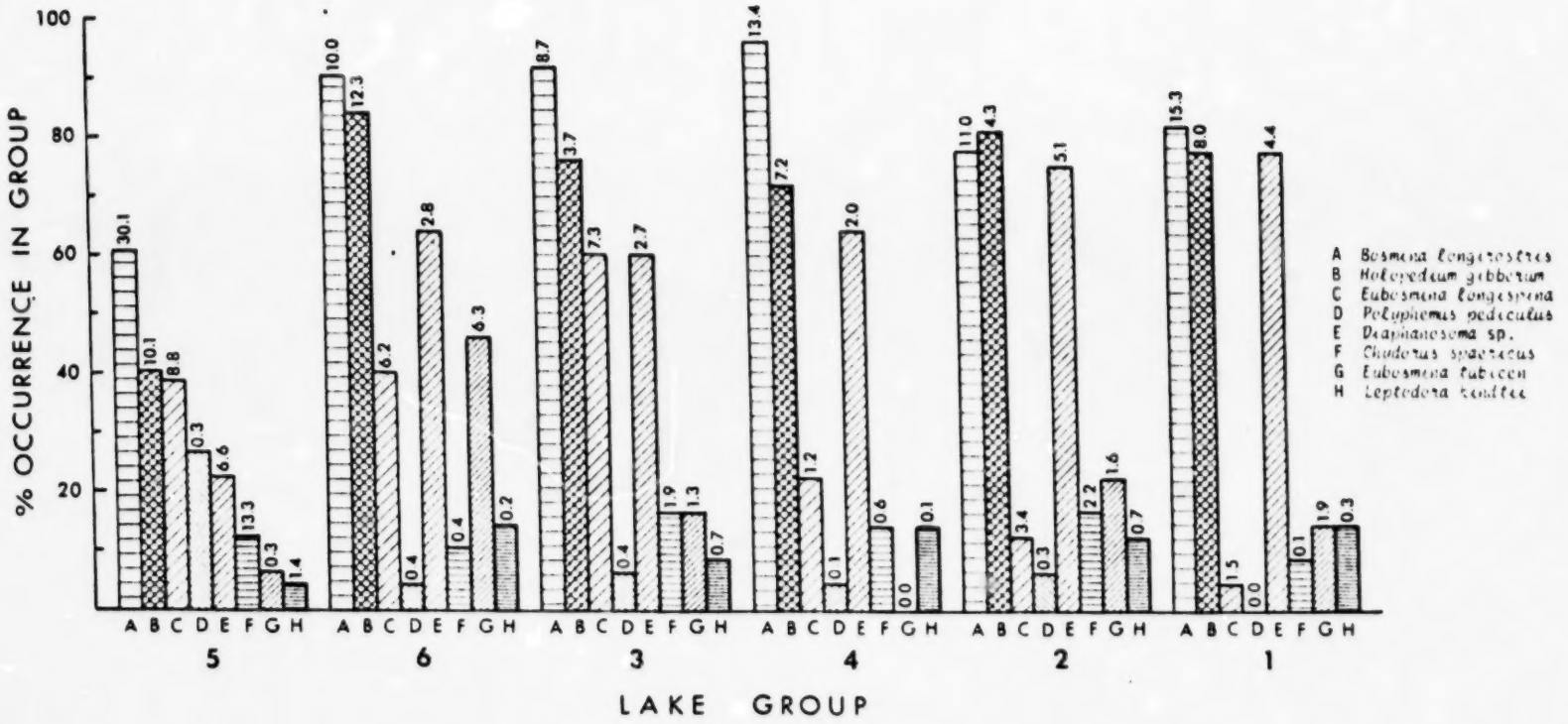

Figure 5. Frequency of occurrence and average % contribution when present of common Cladocera (excluding Daphnidae).

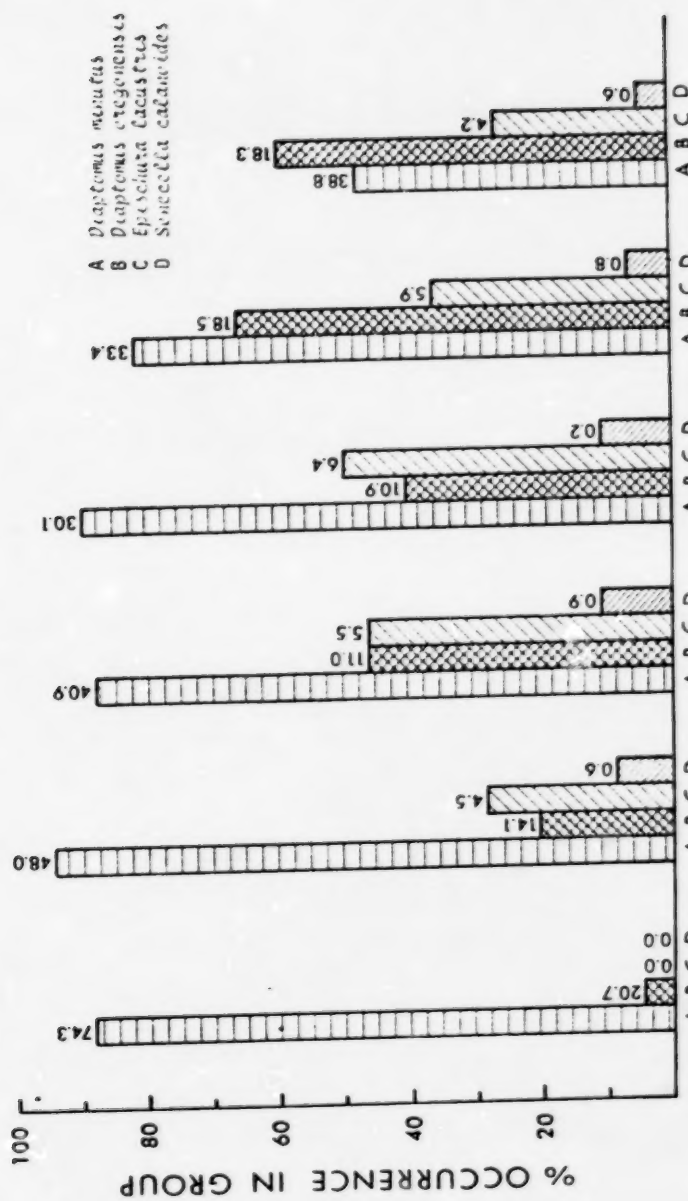

Figure 6. Frequency of occurrence and average % contribution when present of common Calanoida.

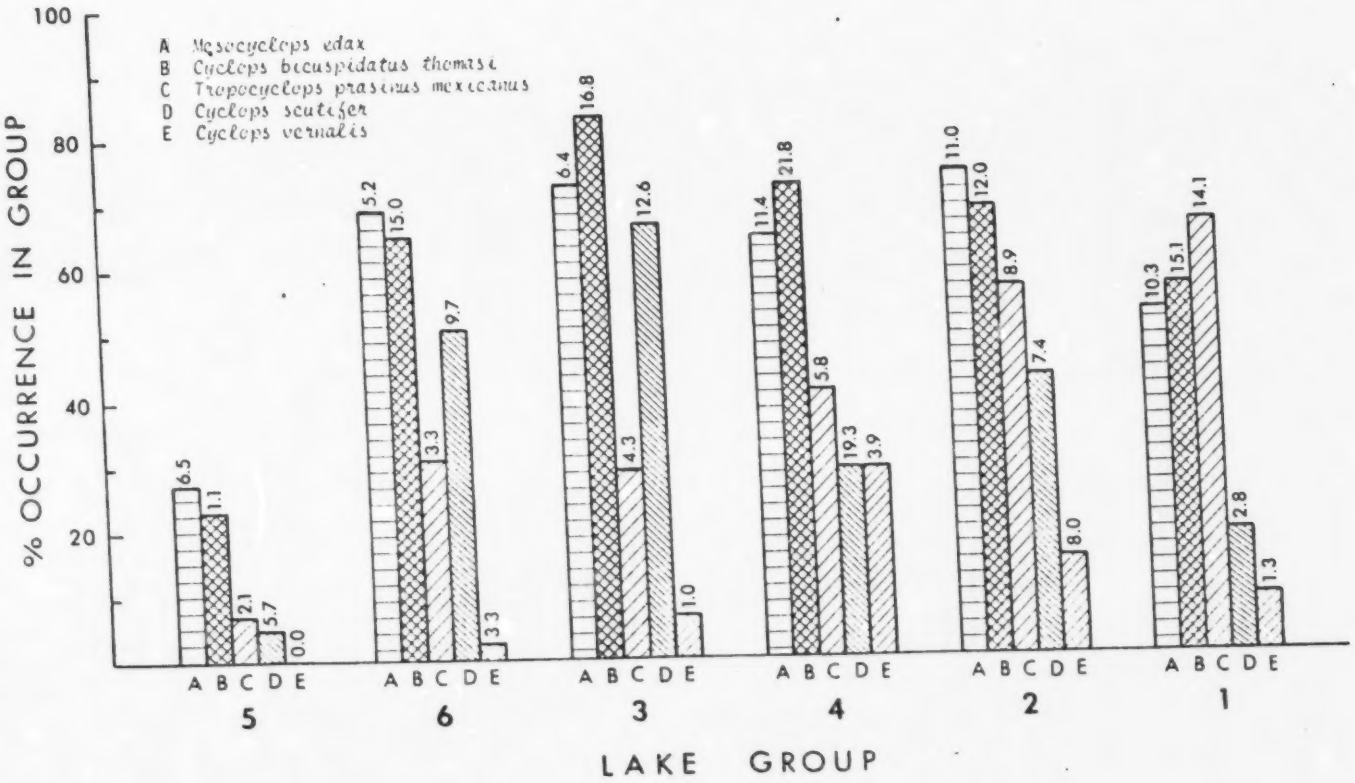

Figure 7. Frequency of occurrence and average % contribution when present of common Cyclopoida.

Cladocera

Several authors (Almer *et al.* 1974; Sprules 1975, and others) have reported scarcity or absence of *Daphnia* in acidic lakes. Our data support these findings, but indicate variation in the environmental preferences of the species of Daphnidae collected (Figure 4). *D. catawba* and *D. ambigua* showed variation in importance between lake groups but demonstrated no obvious declines in acidic lakes (Group 5). Sprules (1975) indicated that *D. catawba* occurs primarily at low pH in LaCloche Mountain lakes and Carter (1971) has documented *D. ambigua* as the predominant cladoceran in four acidic (pH 4.0 to 5.0) ponds near Georgian Bay.

Other Daphnidae collected during our study showed markedly reduced importance in acidic lakes, considering both frequency of occurrence and relative abundance (Figure 4). Of these daphnids, *D. longiremis* was most common in near-neutral oligotrophic lakes (Groups 3 and 4) although the species reached highest relative abundance in the most productive lakes (Group 1). *D. g. mendotae* was consistently important in near-neutral lakes of all types but increased slightly in occurrence and relative abundance among Group 4 and 2 lakes. *D. retrocurva* was most prominent in the most productive lakes and showed generally increasing occurrence and relative abundance with increasing trophic status. *D. dubia* and *D. pulex* were most common in nutrient poor

Group 3 lakes but varied widely in relative abundance among the lake groups. C. lacustris was conspicuously more important in the most productive lakes (Group 1).

B. longirostris, H. gibberum, and Diaphanosoma sp., the most common Cladocera in the study lakes (Table 2), were important among all lake groups. Although frequency of occurrence of these species was somewhat reduced among acidic lakes (Group 5), when present, they contributed substantially to the communities (Figure 5). In the case of B. longirostris and Diaphanosoma sp. maximum relative abundances were reached in acidic lakes. Sprules (1975) has indicated that these species are distributed essentially without regard to pH in LaCloche Mountain lakes.

E. longispina was most common and abundant among highly oligotrophic lakes, including acidic lakes, and was much less prominent among more productive lakes (Groups 4, 2, and 1). E. Tubicen was absent from Group 4 lakes and also from Group 7 lakes (not depicted in Figure 5) which exhibited the hardest waters of our study lakes (Table 1) confirming the observation of Carter et al. 1980 that this species is restricted to very soft waters.

C. sphaericus and P. pediculus were present in lakes of all types (with the exception of Group 1 lakes which contained no P. pediculus) but showed increased importance among

acidic lakes. C. sphaericus has previously been reported as important in acid, metal-contaminated lakes near Sudbury (Yan and Strus 1980), and Sprules (1975) has indicated that P. pediculus occurs primarily at low pH in LaCloche Mountain lakes.

L. kindtii showed generally low abundance in our study lakes, similar to results obtained from surveys of ponds near Georgian Bay (Carter 1971) and the ELA lakes of northwestern Ontario (Patalas 1971). The particular scarcity of L. kindtii among our Group 5 lakes generally agrees with the data of Sprules (1975) which indicated absence from lakes with pH <5.0.

Calanoida

D. minutus was the most common and abundant copepod in the study lakes (Figure 6). The importance of D. minutus was greatest in the most acidic, most oligotrophic Group 5 lakes where, when present, it comprised on average 74.3% of the crustacean density (excluding nauplii). Within other lake groups the average contribution of D. minutus to density ranged from 30.1% to 48.0%. D. minutus was less common in productive Group 1 lakes (47.8%) than in lakes of other groups (81.6 to 94.7%). D. minutus has been previously reported as very important in non-acidic (Schindler and Noven 1971) and acidic (Sprules 1975) oligotrophic

Precambrian Shield lakes. Sprules (1975) has indicated that D. minutus is the only species which remains in some very acidic LaCloche Mountain lakes.

In contrast to D. minutus, D. oregonensis was rare in Group 5 lakes, and showed increasing occurrence and relative abundance with increasing trophic status. D. oregonensis is the predominant calanoid copepod in eutrophic Kawartha lakes, Ontario (Hitchin 1976) and it has been shown to replace D. minutus after artificial fertilization (nitrogen and phosphorus) in a small, near-neutral Sudbury area lake (Yan and LaFrance 1982). E. lacustris and S. calanoides were conspicuously absent from Group 5 lakes.

Cyclopoida

Studies in Scandinavia (Nilssen 1980), the USA (Confer et al. 1983) and Ontario (Roff and Kwiatkowski 1977) have reported a general scarcity of cyclopoids in acidic lakes, agreeing well with our data. Cyclopoids were much less common in Group 5 lakes than in lakes of other groups (Figure 7). Twenty-eight percent of Group 5 lakes had no cyclopoids in the collections (group average 0.9 cyclopoid species/lake) while within other lake groups only from 0 to 5.3% of the lakes contained no cyclopoids with group averages of 2.2 to 2.6 cyclopoid species/lake. C. scutifer was most prominent in oligotrophic, slightly acidic to near-neutral lakes (Groups 6 and 3) while T. p. mexicanus

showed an apparent preference for more nutrient rich waters (Groups 2 and 1). Among near-neutral lakes C. b. thomasi and M. edax were important in all lake groups. C. vernalis occurred much less frequently and was not collected from Group 5 lakes, although previous sampling in the study area has shown the presence of C. vernalis in some of these acidic lakes (Keller 1981).

Although showing reductions in occurrence and relative abundance in our acidic lakes, important populations of cyclopoids do occur at low pH. M. edax and C. vernalis respectively have been identified as the dominant predatory plankton in acidic Cheat Lake which is affected by acid mine drainage (Janicki and DeCosta 1979) and Clearwater Lake which is very close to the Sudbury smelters and has highly elevated Cu and Ni concentrations in addition to low pH (Yan and Strus 1980).

INTERSPECIFIC ASSOCIATIONS

Cluster analysis (Figure 8) indicated that the study lakes were typified by a single major species group common to most lakes and containing D. minutus, B. longirostris, H. gibberum and M. edax. These species were also present in the major recurrent group defined by Sprules (1975) for LaCloche Mountain lakes which in addition contained

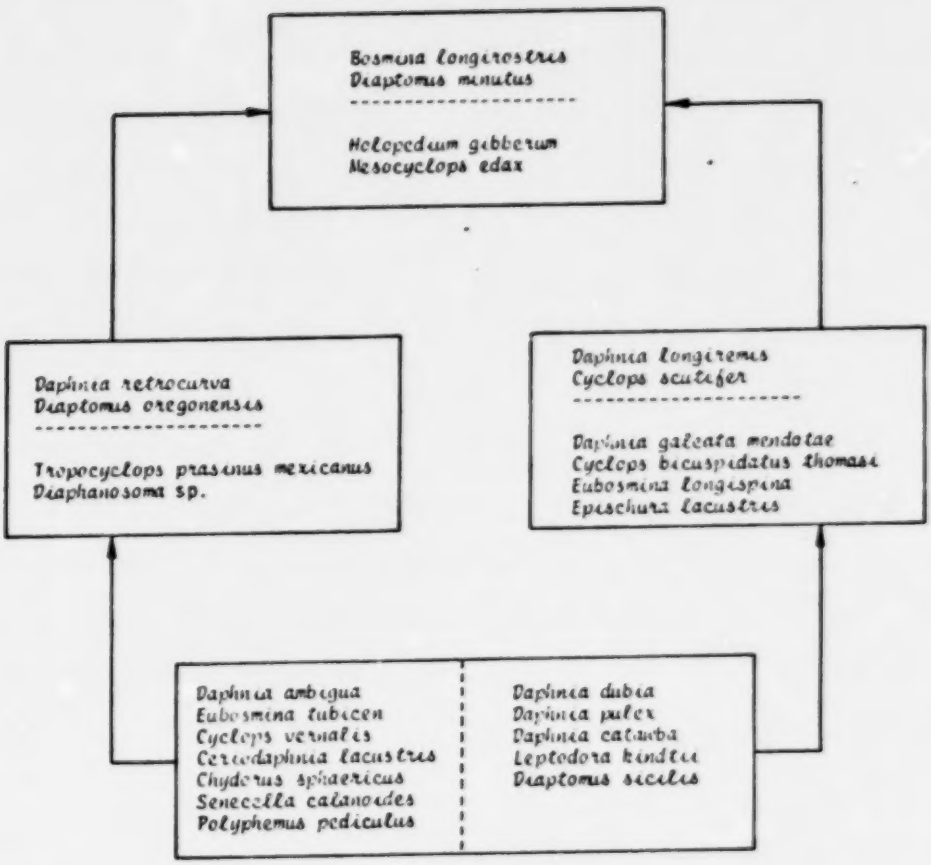

Figure 8. Results of species cluster analysis.

Diaphanosoma sp. and C. b. thomasi. In our analysis, the latter two species were assigned to different species subgroups (Figure 8). One subgroup was characterized by D. retrocurva and D. oregonensis in association with T.p. mexicanus and Diaphanosoma sp. while the other was characterized by D. longiremis and C. scutifer in association with D.g. mendotae, C.b. thomasi, E. longispina and E. lacustris. On the basis of the apparent environmental preferences of their constituent species (Figures 4 to 7) the species subgroups may be generally categorized as groups typical of more productive waters and less productive waters, respectively.

The remaining species shown in Figure 8 were too scarce to permit discrimination by cluster analysis; however, based on the frequency of their co-occurrence with the major species in the subgroups, they have been divided into those species which appear most important in the communities of more productive and less productive lakes respectively. Often the division between these species was very indistinct.

GENERAL COMMUNITY STRUCTURE

If viewed from a functional standpoint, our acidic lakes exhibit basic differences in community structure in comparison to near-neutral lakes (Figure 9). The most conspicuous alterations include: a substantial reduction in

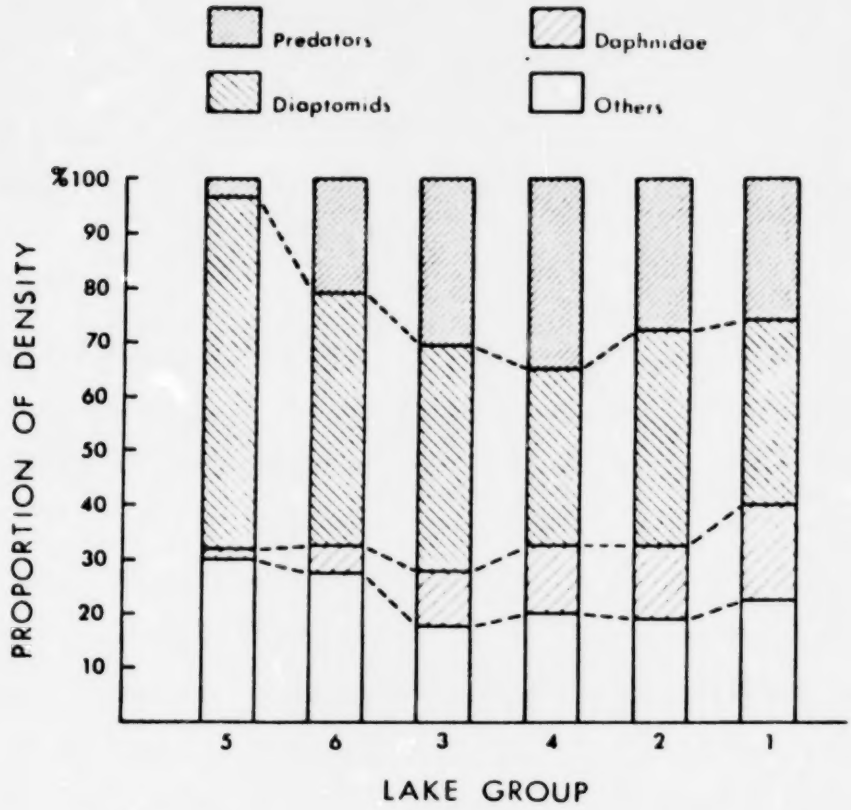

Figure 9. Average % contribution to total density (excluding nauplii) by predators (Cyclopoida, P. pediculus, L. kindtii and E. lacustris), Diaptomids, Daphnidae and other Crustacea in lake groups defined by water chemistry.

the importance of Daphnidae and a concomitant increase in the relative abundance of smaller grazers (particularly D. minutus); and generally reduced abundance of crustacean predators (L. kindtii, E. lacustris and cyclopoids).

On average, Daphnidae comprised only 1.6% of the crustacean density in Group 5 lakes and 4.0% in Group 6 lakes while in other lake groups the average contribution to density ranged from 10.4 to 17.0%. In near-neutral lakes, the relative abundance of Daphnidae showed a general increase with increasing lake trophic status. Other cladoceran grazers (B. longirostris, H. gibberum, Diaphanosoma sp. and E. longispina) showed increased relative abundance among Group 5 and Group 6 lakes (average combined percentage of density 26.7 and 23.6 respectively) in comparison to other lake groups (16.2 to 23.6%).

Predators (including omnivorous species) comprised only 2.7% of the average crustacean density in acidic Group 5 lakes and from 20.5 to 27.8% in other lake groups while diaptomids comprised 65.7% of the average density in Group 5 lakes and from 31.9 to 48.0% in other groups.

The general tendency toward increasing importance of smaller crustacean plankters in acidic lakes is apparent when communities are considered on the basis of average size class composition (Figure 10). In Group 5 lakes only 5.4%

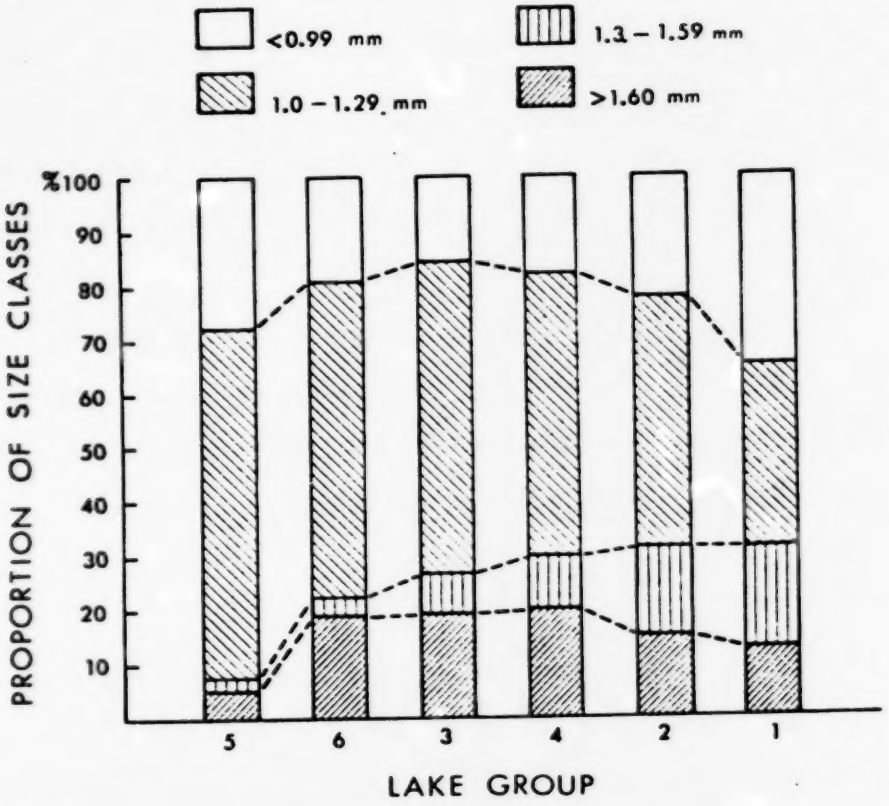

Figure 10. Average % contribution to total density by size classes of crustacean plankton. The four size classes depicted are a condensation of the six categories reported by Roff et al. (198[illegible]). Assignment of species to categories followed Roff et al. (1981).

of the average crustacean density was comprised of species with an adult body length $\geq$ 1.6 mm while this size category accounted for 12.9 to 20.0% of the individuals in other lake groups. Species in the intermediate size ranges (1.0 to 1.59 mm adult body length) were well represented in all lake groups (52.6 to 68.2% of average density). Of these, species in the 1.0 to 1.29 mm size range were most prominent in acidic Group 5 lakes (67.3% of average density) due largely to the inclusion of D. minutus in this category, and showed decreasing importance (60.3 to 34.3% of average density) with increasing trophic status. Species in the size range of 1.3 to 1.59 mm (predominantly D. retrocurva and D. oregonensis) were very unimportant in Group 5 lakes (0.9% of average density) and increased in importance with increasing trophic status (3.6 to 18.3% of average density). Small species (<1.0mm) comprised on average 26.4% of the density in Group 5 lakes and 15.7 to 19.2% in other lake groups (excluding Group 1). Interestingly, the highest relative proportion of small (<1.0 mm) species (30.2%) occurred in the most productive Group 1 lakes.

It is noteworthy that the apparent tendency toward increasing importance of smaller taxa in acidic lake occurs not only in general, but is manifested within genera i.e. D. minutus increases in importance in acidic lakes while the larger D. oregonensis declines and of the daphnids the species which do not appear adversely affected in acidic lakes (D. catawba, and D. ambigua) are small representatives of the genus.

Although biomass was not measured in our study, the increased importance of smaller taxa (Figure 10) and low density (Figure 3) in Group 5 lakes indicates reduced crustacean biomass under acidic conditions.

ENVIRONMENTAL INFLUENCES

The mechanisms of community alteration in acidic lakes are unclear, and may be diverse. The abrupt declines of some large species (ie. most Daphnia, S. calanoides, and the predaceous L. kindtii and E. lacustris) in acidic lakes imply direct toxicity by pH or a related variable, but other lake characteristics may be implicated. The increased importance of some cladoceran grazers (B. longirostris H. gibberum and Diaphanosoma sp.) in some acidic lakes suggests a response to reduced competition from Daphnia. It has been shown that Daphnia can depress Bosmina populations (DeMott and Kerfoot 1982; Goulden, Henry and Tessier 1982). As suggested by Sprules (1975) the increased importance of P. pediculus in acidic lakes may reflect reduced competition from other predatory plankton. The reduction in importance of Cyclopoida in acidic lakes is confusing since cyclopoids generally seem tolerant of low pH (Lowndes 1952) and species common in our study area are at least occasionally important in highly acidic lakes. The generally very low productivity of our acidic study lakes may be implicated, since Neill and Peacock (1980) demonstrated high springtime mortality of juvenile c.b. thomasi at low food levels.

Eriksson et al. (1980) have suggested that with acidification and resultant elimination or reduction of fish predation the zooplankton grazing community shifts to dominance by larger species (particularly larger Calanoida) with a corresponding decrease in the importance of smaller Cladocera. These observations do not appear to hold true for our lakes in which the increased importance of Calanoida (D. minutus) is strongly associated with declines in the larger Daphnia species, and smaller Cladocera (notably B. longirostris) remain important. Further, although some large species such as H. gibberum may be important at low pH, a strong tendency toward dominance by smaller Crustacea (D. minutus and B. longirostris) remains evident even in the most acidic lakes which are completely devoid of fish populations.

Stepwise multiple linear regression analysis of selected (see methods) limnological variables against the percent contribution of individual species failed to explain much of the variation in species proportions (Table 3). Within near-neutral lakes (Groups 1, 2, 3, 4) on average only 11% of the variation in species proportions could be explained by the "best" (based on order of occurrence in the regression equation) five or less predictive variables for each species. Considering the range of lakes over which the biological effects of acidification are manifested (Groups 5 and 6) five or fewer physico-chemical variables accounted

TABLE III

Results of stepwise multiple linear regressions of limnological variables against % contribution of common crustacean plankton species to total density (excluding nauplii).

Species[a]	Lake Groups	Variables[b,c,d]	Multiple r[e]	Species[a]	Lake Groups	Variables[b,c,d]	Multiple r
D. minutus	1, 2, 3, 4	SD, pH-, Ao, TIA-, TN-	0.34***	T.p. mexicanus	1, 2, 3, 4	DT, TP, pH, SD-, Cu	0.43***
	5, 6	SD, Cu-, DT, pH-, TP-	0.62***		5,6	DT, pH, TP, ET, TN-	0.40**
B. longirostris	1, 2, 3, 4	Cu, SD-, pH, TP, ET-	0.40***	E. lacustris	1, 2, 3, 4	DT-, pH, TN-	0.20*
	5, 6	DE-, TN-, Cu, TP, pH-	0.41**		5, 6	TIA, AL-, SD-, Cu-, TN	0.70***
H. gibberum	1, 2, 3, 4	DT, ET-, TN, Cu, TP	0.39***	E. longispina	1, 2, 3, 4	SD, DE, TIA-, Ao, TN-	0.49***
	5, 6	ET-, HT-, DT-, TIA-, pH	0.43**		5, 6	TN-, DE, HT, TP-, Al	0.49***
C. b. thomasi	1, 2, 3, 4	DT-, pH, Al, DE, SD	0.43***	D. catawba	1, 2, 3, 4	pH-, DE-, SD, HT-, TIA-	0.45***
	5, 6	pH, DT-, TN, ET, SD-	0.63***		5, 6	-	-
M. edax	1, 2, 3, 4	pH-, HT-, TN-, TP, ET	0.35***	D. ambigua	1, 2, 3, 4	-	-
	5, 6	pH, TN, SD-, DT-, Ao	0.41**		5, 6	TN, DT-, DE-, TIA-, HT-	0.38**
Diaphanosoma sp.	1, 2, 3, 4	SD-, ET-, Ao-, Cu-, pH-	0.27*	D. pulex	1, 2, 3, 4	DT, pH, ET-, Cu-	0.24*
	5, 6	DT, Al-, Cu, pH-, TN	0.47***		5, 6	-	-
D.g. mendotae	1, 2, 3, 4	pH, TP, Ao, Cu-, SD-	0.27*	C. sphaericus	1, 2, 3, 4	pH, DT, TP-, SD-, ET	0.32**
	5, 6	TIA, pH, TN, DT-, HT-	0.44***		5, 6	Cu, Al, pH-, TIA-, ET	0.94**
D.retrocurva	1, 2, 3, 4	DE-, TP, SD-, TN, DT	0.34***	D. dubia	1, 2, 3, 4	TN-, pH, TIA-, ET, SD	0.36***
	5, 6	TP, pH, DT, TN-, ET-	0.40**		5, 6	pH, TP-, Ao, Cu-, SD-	0.37**
C. scutifer	1, 2, 3, 4	SD, Ao, ET, HT, TIA	0.48***	L. kindtii	1, 2, 3, 4	DT, ET	0.18*
	5, 6	HT, SD-, TN-, ET-, Cu-	0.60***		5, 6	Ao, HT-, TP-, Al-, ET	0.50***
D. oregonensis	1, 2, 3, 4	ET-, TN, Cu-, pH-, Ao-	0.28**	C. lacustris	1, 2, 3, 4	TP, Cu-, TN, pH, Ao-	0.26*
	5, 6	TIA, TN, Ao-, pH, DT-	0.42***		5, 6	TIA, pH, HT-, SD-, Cu-	0.56***
D. longiremis	1, 2, 3, 4	DT-, DE, ET-, pH, Al	0.26*	P. pediculus	1, 2, 3, 4	-	
	5, 6	pH, ET, DT-, TIA, SD-	0.56***		5, 6	SD, ET-, DT, Al, pH-	0.42***
S. calanoides	1, 2, 3, 4	HT, pH, DT-, DE, ET	0.34***				
	5, 6	TIA, Ao-, TN, HT	0.33*				

[a] only species present in >5% of the study lakes included; E. tubicen and C. vernalis are excluded since meaningful statistics could not be generated for these species

[b] pH = pH; TIA = alkalinity; Al = Al; Cu = Cu; TN = total nitrogen; TP = total phosphorus; SD = Secchi disc; DE = bottom depth; HT = hypolimnion thickness; ET = epilimnion thickness; Ao = lake area; DT = deep-water temperature

[c] minus sign indicates variables which exhibited a negative relationship

[d] where fewer than five variables are listed additional variables could not be added and retain signficance at P<0.1; where no variables are listed no relationships were significant at P<0.1

[e] levels of significance; *** = P<0.01; ** = P<0.05, * = P<0.1

for, on average, 25% of the variation in species proportions. The somewhat enhanced predictive ability in highly and intermediately acidic lakes may suggest increased importance of abiotic factors as controls on species composition.

The generally poor statistical resolution of relationships between physio-chemical variables and species proportions may reflect in part our lack of consideration of biological influences (fish and invertebrate predation; competition) in the analysis. However, Roff et al. (1981) generally found little statistical correlation between zooplankton species abundances and abundance of predatory plankton species and presence/absence of planktivorous fish and interpreted this to suggest that such biological controls may not be intense in the larger lakes predominant in their study. This conclusion, if verified, would be applicable to our lakes which tend to be reasonably large (Table 1). Alternately, the lack of high statistical resolution in our data may reflect the difficulties of using only point in time data (particularly for biological characteristics which may show wide temporal variation) which may not completely reflect conditions on an individual lake basis.

Although much of the variation in species proportions could not be explained on the basis of physico-chemical variables, examination of those variables apparently most important,

based on regression analysis, is instructive. Within near-neutral lakes (Groups 1, 2, 3, 4) a characteristic related to lake thermal structure (epilimnion thickness, hypolimnion thickness or deep-water temperature) emerged as the best single predictor of species proportions for 9 out of 21 species. These included H. gibberum, C. b. thomasi, D. oregonensis, D. longiremis, T. p. mexicanus, E. lacustris, D. pulex, L. kindtii and S. calanoides. Although it has been shown that lake acidificaton may result in increased water clarity and attendant changes in thermal structure (Harvey et al. 1981), among Group 5 and 6 lakes only 4 species (H. gibberum, Diaphanosoma sp., C. scutifer and T. p. mexicanus) were best correlated with a thermal characteristic while for 9 species (C. b. thomasi, M. edax, D. g. mendotae, D. oregonensis, D. longiremis, E. lacustris, D. dubia, C. lacustris and S. calanoides), including most of the species exhibiting substantial declines in acidic lakes, pH or the closely related alkalinity (also a measure of lake acidity) appeared as the primary correlates with percent composition. Lake pH also emerged as the single best correlate with total number of species ($r=0.71$; $P<0.01$) in lake groups 5 and 6.

Considering other variables, in near-neutral lakes the relative proportions of 4, 2, 1 and 1 species, respectively, were best correlated with Secchi disc transparency, nutrient (total phosphorus, total nitrogen) concentrations, Cu

concentrations and lake depth respectively. Two, 3, 1, 1, and 1 species respectively were best correlated, in turn, with Secchi disc transparency, nutrient concentrations, Cu concentrations, depth and area in Group 5 and 6 lakes.

Given the elevated trace metal concentrations in many of our study lakes it is surprising that trace metal data did little to explain species proportions. Only two species (B. longirostris and C. sphaericus) both of which have previously been shown as important under highly acidic, metal contaminated conditions (Yan and Strus 1980) showed Cu as a primary correlate, and in both cases the correlation was positive. The increased relative abundance of B. longirostris in Cu and Ni contaminated lakes suggests that this species is more tolerant of very high metal concentrations than D. minutus, the more common acid lake dominant. Although Al has been strongly implicated in fish mortalities under acidic conditions (Baker and Scofield 1980; Muniz and Lievestad 1980) total Al concentrations did not emerge as the single best predictor of percent composition for any species; although Al did occupy second position in the regression equation for Diaphanosoma sp., E. lacustris and C. sphaericus.

Morphometric characteristics accounted for little of the variation in species percent composition, suggesting that the generally observed correlations between lake size and

depth and zooplankton communities (Patalas 1971; Sprules 1975) may largely reflect other factors such as thermal structure and general lake trophic status which are closely linked to morphometry. It must be noted however, that many of the morphometry-related changes in zooplankton abundance and community structure suggested by Patalas (1971) occurred in lakes characteristically much smaller than those sampled in our study.

CONCLUSIONS

Crustacean plankton assemblages in northeastern Ontario lakes largely reflect general water quality, particularly characteristics associated with lake trophic status and degree of acidification.

Overall, the lakes are characterized by a major group of very common species (*B. longirostris*, *D. minutus*, *H. gibberum* and *M. edax*) and two species subgroups which show apparent lake type preferences. Considering the frequency of occurrence, and average percent composition of species in lake groups defined by water chemistry, *D. retrocurva*, *D. oregonensis*, *T. p. mexicanus* and *Diaphanosoma* sp. comprise a species subgroup which is most prominent in more productive lakes while a second subgroup including *D. longiremis*, *C. scutifer*, *D. g. mendotae*, *C. b. thomasi*, *E. longispina* and *E. lacustris* is most

important in less productive lakes. It is important to note that among near-neutral lakes the observed environmental preferences of species were manifested as gradual changes in occurrence and relative abundance over a range of lake types, not as abrubt changes between lake types. Among acidic lakes, which are common in the study area, crustacean plankton communities showed low density and reduced numbers of species related to reduced importance of larger grazers (Daphnidae) and predators (Cyclopoida, L. kindtii and E. lacustris).

Our synoptically collected data shed little light on the actual mechanisms of community alteration. However, the results of stepwise multiple linear regression analyses of species proportions against limnological characteristics suggest that of the physico-chemical variables considered, characteristics related to thermal structure may be very important in near-neutral lakes while actual lake acidity may be the primary control in acidified lakes.

It is hoped that the data provided herein will provide a framework for more detailed consideration of the influences of acidification on crustacean plankton in Precambrian shield lakes, and underscore the need for more temporally rigorous, quantitative study.

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